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Effects of *Ageratina adenophora* Invasion on the Understory Community and Soil Phosphorus Characteristics of Different Forest Types in Southwest China

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Abstract: Understanding the influence of invasive species on community composition and ecosystem properties is necessary to maintain ecosystem functions. However, little is known about how understory plant communities and soil nutrients respond to invasion under different land cover types. Here, we investigated the effects of the invasive species *Ageratina adenophora* on the species and functional diversity of understory communities and on soil phosphorus (P) status in three forest types: CF, coniferous forest; MF, coniferous and broadleaf mixed forest; and EBF, evergreen broadleaf forest. We found that the species and functional diversity indices of the understory community significantly varied by forest type. Among the invaded plots, the greatest decrease in functional diversity (functional richness, functional divergence, and functional dispersion) and biotic homogenization were found in the CF rather than the MF or EBF. In addition, the invasion by *A. adenophora* significantly increased the soil $NaHCO_3$-extractable inorganic P and organic P in the MF and EBF, respectively, while obviously decreasing the soil maximum P sorption capacity and maximum buffering capacity in the CF. However, the changes in the species and functional attributes of the understory communities were weakly associated with changes in the soil P status, probably because of the different response times to invasion in different forest types. The implication of these changes for ecosystem structure and function must be separately considered when predicting and managing invasion at a landscape scale.

Keywords: biological invasion; functional diversity; understory community; soil phosphorus fractions; soil phosphorus sorption characteristics

1. Introduction

Alien plant species invasion is recognized as a serious threat to biodiversity and ecosystem functions [1–3]. Invasive plants can affect natural and semi-natural habitats by displacing native species and changing the nutrient status of the soil [4,5]. Some studies have reported that non-native species invasion may affect terrestrial ecosystem processes and functions via changes in plant community

composition or soil properties [6,7]. However, many of the observed impact patterns may depend on many confounding factors of the landscape, including the influence of different land cover types [8]. Thus, understanding the influence of invasive species on biodiversity and ecosystem functions in different land cover types can improve spread predictions and reduce ecosystem impacts due to invasive plant species.

The effect of invasion is frequently associated with biodiversity loss; however, changes in the plant species composition and diversity may take many years to play out, especially in forest ecosystems. However, increasingly, research is devoted to plant functional traits, exploring how changes in the functional attributes of plant communities affect ecosystem functions and their response to environmental changes [9,10]. Furthermore, trait-based approaches are being used to examine how invasion affects ecosystem structure and functions [11,12]. In forest ecosystems, invasive species may have a detrimental effect on the understory vegetation, which in turn plays a critical role in ecosystem functions [13,14]. Hence, analysing the response of plant functional attributes within the understory community to invasion and the relationships between functional attributes and ecosystem functions might help detect early vegetation responses and ecosystem function alterations. However, the responses of plant functional attributes to invasion and their feedback to ecosystem processes and functions is likely to vary among different forest types.

Among ecosystem processes and functions, the effect of invasion on the soil phosphorus (P) cycle is less understood than the effect of invasion on the carbon (C) and nitrogen (N) cycles [15–17]. Most studies on the modification of the P cycle due to exotic species typically focus on the total P (TP) and inorganic P (Pi) forms [18], and less data exist on the impacts of exotic plants on P fractions and P dynamics. Among soil P fractions, Pi extracted with deionized water (water-Pi) and $NaHCO_3$ (bicarb-Pi) are considered the most biologically and readily available Pi forms, and Po extracted with $NaHCO_3$ (bicarb-Po) is easily mineralizable and may contribute to plant-available Pi [18]. In invaded ecosystems, exotic species can affect the distribution and fluxes of easily available P in soil at short- and medium-term time scales, by changing the soil microbial community or soil physicochemical properties [19–21]. However, different patterns of changes in the soil P fraction have been observed in some studies, because the direction and degree of changes in P cycling may depend on many confounding factors, including the specifics of site conditions, land use type, and the biological characteristics of exotic species [22–24]. Therefore, the measurement of easily available P and P behaviour characteristics, together with vegetation properties, is required to better understand the relationships among invasion, vegetation composition, and soil P cycling.

The invasive herb *Ageratina adenophora*, a perennial shrub native to Mexico, invaded China in the 1940s from Burma and is now widespread in Southwest China [22]. In this region, invasion by *A. adenophora* has a profound influence on the composition, structure, and function of the impacted forest ecosystems because of its clonal reproduction and competitive advantage [16,25]. However, there are few quantitative data on the effects of *A. adenophora* on understory community composition and soil P status in different forest types. In this study, three typical forest types in Xishan National Forest Park bordering Dianchi Lake, a substantially eutrophic water body in Southwest China, were selected to investigate the invasion effect on understory communities and soil P status, P fraction and P sorption characteristics. Our aims were (1) to determine the effects of invasion by *A. adenophora* on the understory plant community and soil P status (including the easily available P fractions and P sorption characteristics) in the three forest types, and (2) to quantify the effects of invasion on the relationships between understory plant community properties and soil P status.

2. Materials and Methods

2.1. Site Description

The study was carried out at Xishan National Forest Park (102°37~38′ E, 24°57~59′ N), nearby Kunming city, Yunnan Province, China. This park borders Dianchi Lake to the east. Owing to the

influence of the southwestern monsoon climate, the average annual precipitation in the area is 1100 mm. The rainy season lasts from May to October each year. The mean annual temperature is 14.7 °C. The soils in the study area are classified as Cambisols (according to FAO/UNESCO classifications), which developed from basalt parent material. The original vegetation was a semi-humid evergreen broadleaved forest, some of which was utilized as coppices for fuelwood after deforestation before the 1960s. Since the 1980s, some of these have been planted by *Pinus armandii* and *P. yunnanensis* after deforestation. Due to the long-term preservation of some original vegetation and different restoration measures, the diversity of vegetation shows a patchy distribution. The main vegetation types are semi-humid evergreen broadleaf forest, coniferous and broadleaf mixed forest, and subtropical coniferous forest. In this area, these three forest types with similar conditions, according to topography, slope, and direction, were selected for community investigation and soil sampling: (1) coniferous forest (CF), dominated by *P. armandii*; (2) coniferous and broadleaf mixed forest (MF), dominated by *Castanopsis delavayi* and *Keteleeria evelyniana*; and (3) evergreen broadleaf forest (EBF), dominated by *Cyclobalanopsis glaucoides*. The locations of the sampling plots and the details of the plant community characteristics and basic soil properties are shown in Figure 1 and Table 1.

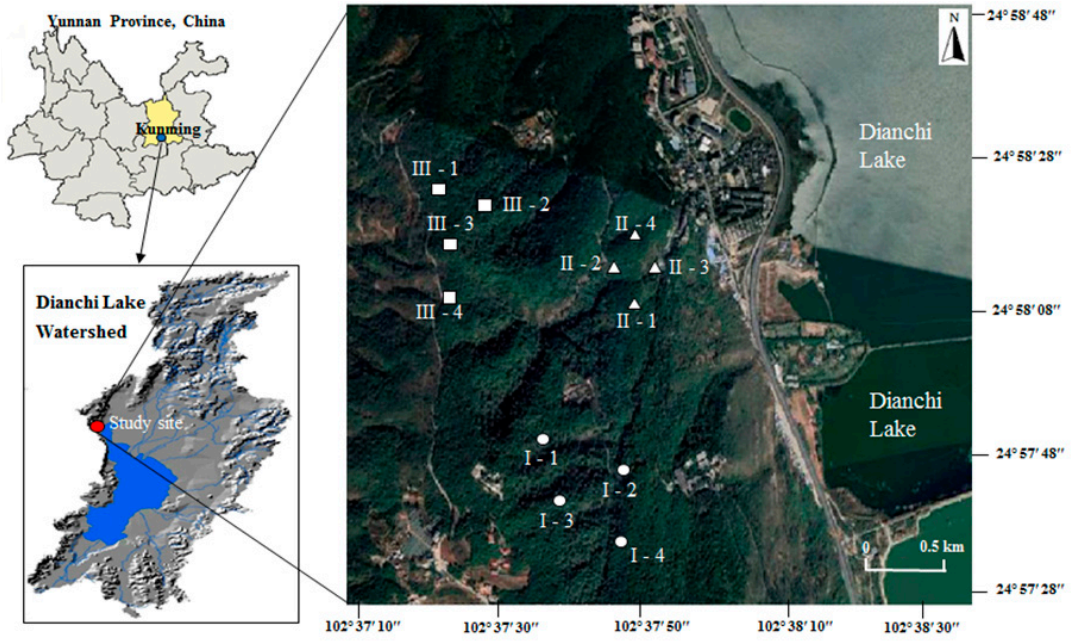

Figure 1. Map of the study site and the four sampling plots in each forest type (I, coniferous forest; II, coniferous and broadleaf mixed forest; III, evergreen broadleaf forest).

Table 1. Community structure and the basic soil properties of the three forest types in the study sites.

		CF	MF	EBF
Tree layer				
Coverage		0.66 ± 0.02b	0.78 ± 0.04a	0.82 ± 0.03a
Height (m)		9.75 ± 0.48b	16.00 ± 0.41a	15.00 ± 0.41a
Basic soil properties				
pH	Invaded	4.53 ± 0.03a	4.37 ± 0.04b	4.27 ± 0.06b
	Uninvaded	4.57 ± 0.03a	4.39 ± 0.05b	4.26 ± 0.05b
SOC (g kg^{-1})	Invaded	39.17 ± 1.49c	45.25 ± 1.17 b	49.93 ± 0.23a
	Uninvaded	37.82 ± 1.02c	43.76 ± 0.82b	47.77 ± 0.91a
TN (g kg^{-1})	Invaded	0.74 ± 0.04b	1.19 ± 0.07a	1.44 ± 0.12a
	Uninvaded	0.67 ± 0.07b	1.08 ± 0.09a	1.32 ± 0.09a

Values are the mean ± standard error. Different letters indicate significant differences between forest types based on an LSD test ($p < 0.05$). CF, coniferous forest; MF, coniferous and broadleaf mixed forest; EBF, evergreen broadleaf forest; SOC, soil organic carbon; TN, total nitrogen.

2.2. Community Investigation and Soil Sampling

For each forest type, four sets of paired sampling plots (uninvaded and invaded plots) (15 m × 15 m) were selected for vegetation investigation and soil sampling. Due to the different intensities of invasion in the three forest types, plots with similar *A. adenophora* coverage (approximately 30%) were chosen as the invaded plots in the three forest types to increase comparability. Adjacent uninvaded plots were used as the reference plots. The uninvaded plots were at least 20 m apart from the invaded plots, and the distance between each pair of plots was greater than 500 m to reduce the effects of spatial autocorrelation. In each plot, four subplots (3 m × 3 m) were used to record the presence and abundance of shrubs, while the herbs and seedlings were enumerated in two nested plots (1 m × 1 m). Then, five important plant functional traits (leaf dry matter content (LDMC), specific leaf area (SLA), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), and specific root length (SRL)) were measured based on at least 5 individuals for each species, following standardized protocols [26].

Based on the floristic inventory, the species diversity (S, richness; H, Shannon diversity; E, evenness) and functional diversity (FD) (FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; FDis, functional dispersion) were all calculated using the FDiversity software package [27] according to the recommendations of Laliberté and Legendre [28]. The FRic is considered as the index that indicates that the resources are potentially available to the community. The FEve and FDiv are used to represent the degrees of resource-effective utilization and competition of some parts of niche space, respectively. FDis is the mean distance of individual species to the centroid of all species in the multidimensional space defined by species traits, accounting for their abundances [28]. Soil samples were collected from 0 to 20 cm because the soil nutrient status in this surface layer is affected by invasion and the understory community to a greater degree. Soil samples were collected at six random locations in each plot, and then they were pooled and sieved (2 mm mesh) for the soil analyses.

2.3. Analysis of Soil P Indicators

Soil total P was determined using the H_2SO_4-H_2O_2 digestion method [29]. Easily available P fractions were obtained by the sequential extraction procedure of Hedley et al. [30], as modified by Tiessen and Moir [31]. Soil samples were extracted with deionized water and 0.5 M $NaHCO_3$ at pH 8.5, which extracts labile Pi (i.e., water-Pi) that is directly exchangeable with the soil solution and labile Pi and Po (i.e., bicarb-Pi and bicarb-Po) held on soil surfaces. Inorganic P concentrations in each extract were determined with a UV-V spectrophotometer using the phosphomolybdate blue method [32]. The total P extracted with $NaHCO_3$ was determined using persulfate digestion. Organic P was estimated as the difference between TP and Pi. To assess the relative contribution of biological processes to the distribution of easily mineralized P in the soil, an index of biologically available P was calculated using bicarb-Po divided by the total of water-Pi, bicarb-Pi, and bicarb-Po [33].

To obtain phosphorus sorption isotherms, 2.5 g of air-dried and sieved soil was suspended in 50 mL of 0.01 M $CaCl_2$ solution containing various initial phosphorus concentrations (0, 10, 20, 40, 80, and 150 mg/L). Three drops of toluol were also added to restrict the activity of microbes. After vigorous shaking for 24 h, the suspensions were filtered (0.45 μm), and the sorbed P was calculated from the difference between the measured equilibrium P concentration of the filtrate and the initial P concentration. The Langmuir equation ($C/S = C/S_m + 1/k \times S_m$) was employed to describe the P adsorption in the soils. In this equation, C, S, S_m, and k represent the equilibrium P concentration, sorbed phosphorus, maximum P sorption capacity, and a constant related to the P binding energy in the solid phase, respectively. In addition, the maximum buffering capacity (MBC) was also calculated as S_m multiplied by k.

2.4. Statistical Analysis

We first used nonmetric multidimensional scaling (NMDS) based on the Bray-Curtis index to visualize the dissimilarity in the understory plant communities between the invaded and uninvaded

plots in the three forest types. NMDS is an effective method in community analysis because it does not assume a linear distribution of the data [34]. The significance of the variations in the composition of the understory plant community was tested by PERMANOVA with Bray-Curtis dissimilarities and 999 permutations. In addition, we used the NODF (nestedness based on overlap and decreasing fill) metric to evaluate the nestedness for the understory species composition in each forest type, aiming to quantify whether depauperate assemblages in invaded plots constituted subsets of progressively richer assemblages in uninvaded plots. The significance of the NODF values compared to random communities was calculated using 1000 randomizations with a fixed–fixed null model, as recommended by Ulrich et al. [35]. Then, two-way ANOVA and *t*-test were performed to assess the significant differences in the understory plant community (species diversity and FD) and soil P status between the invaded and uninvaded plots in the three forest types. Finally, the GLM (general linear model) was applied to elucidate the relationships between the soil P status (as a response variable) and the index of the understory community (as an explanatory variable), with the effects of invasion, vegetation type and the interaction of invasion and the index of the understory community as fixed factors. The interaction term in the GLM allows us to check whether the relationship varied between the invaded and uninvaded communities. When the interaction term was not significant, the GLM was repeated without it to increase the degrees of freedom. Prior to the aforementioned analyses, when the raw data did not meet the normality assumptions, they were log or Box–Cox transformed. NMDS was performed in Canoco 5 (Microcomputer Power, Ithaca, NY, USA). NODF was conducted with the NODF 2.0 program [36]. The other statistical analyses were performed in SPSS (version 19.0; SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Characteristics of the Understory Community

The NMDS analysis and the PERMANOVA revealed that the understory community composition significantly varied by vegetation type ($F = 6.36$, $p < 0.001$), invasion ($F = 7.36$, $p < 0.001$), and their interaction ($F = 9.50$, $p < 0.001$) (Figure 2). The results of the two-way ANOVA also demonstrated that the vegetation type and invasion had significant effects on the species diversity and functional diversity of the understory community (Table 2). Specifically, the vegetation type had a highly significant effect on H, E, FEve, and FDis. Higher values of both H and E were found in the MF. Moreover, the ANOVA revealed a highly significant effect of invasion on S, FRic, FEve, and FDis (Table 2). The values of S, H, FRic, and FDis at the uninvaded plots in CF were all significantly higher than those at the invaded plots (Table 3). The interaction of vegetation and invasion also had a significant effect on FDis, indicating that the impact of invasion on FDis varied depending on the vegetation type (Tables 2 and 3). In addition, the NODF analysis showed that there was significant nestedness in the CF (NODF = 37.97, $p < 0.05$), indicating that the species composition of the invaded plots represents a subset of that in the uninvaded plots. By comparison, the MF and EBF had nonsignificant (i.e., non-nested) results ($p > 0.05$).

Table 2. The results of two-way analyses of variance for the effects of forest type (vegetation) and invasion (uninvaded vs. invaded) and their interaction on the properties of the understory plant community.

	S	H	E	FRic	FEve	FDiv	FDis
Vegetation	3.56	15.40 ***	14.78 **	3.71	6.85 **	2.49	16.20 ***
Invasion	7.10 *	0.29	4.41	9.64 **	4.89 *	1.36	9.57 **
Vegetation × invasion	1.92	3.76	0.19	1.76	0.29	0.77	17.94 ***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. S, richness; H, Shannon diversity; E, evenness; FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; FDis, functional dispersion.

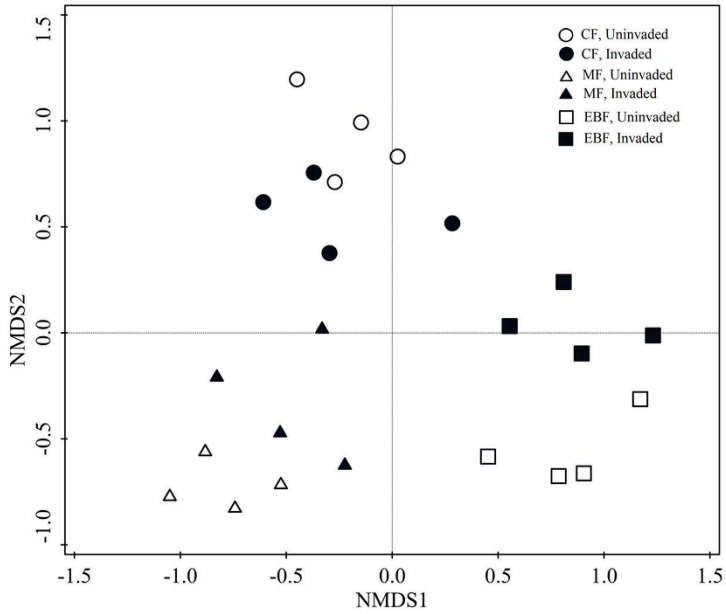

Figure 2. Nonmetric multidimensional scaling (NMDS) of the understory community composition in the invaded and uninvaded sites across three vegetation types (the Bray-Curtis distance metric was used). The points with the same shapes represent the four replicates used in this study.

Table 3. Comparison of the species diversity and functional diversity of the understory communities between the invaded and uninvaded plots in the three forest types.

	CF		MF		EBF	
	Invaded	**Uninvaded**	**Invaded**	**Uninvaded**	**Invaded**	**Uninvaded**
S	9.00 ± 0.58 *	14.67 ± 1.20	11.67 ± 0.67	13.00 ± 1.15	14.33 ± 2.33	15.67 ± 0.88
H	1.16 ± 0.03 *	1.29 ± 0.02	1.31 ± 0.03	1.23 ± 0.03	1.07 ± 0.07	1.07 ± 0.02
E	0.53 ± 0.01	0.48 ± 0.02	0.54 ± 0.01	0.49 ± 0.02	0.41 ± 0.04	0.39 ± 0.02
FRic	11.33 ± 5.51 **	47.68 ± 1.32	15.78 ± 5.36	21.67 ± 3.35	31.05 ± 12.69	50.70 ± 12.82
FEve	0.56 ± 0.02	0.64 ± 0.05	0.46 ± 0.01	0.50 ± 0.04	0.45 ± 0.06	0.53 ± 0.02
FDiv	0.84 ± 0.08	0.93 ± 0.01	0.93 ± 0.01	0.94 ± 0.01	0.96 ± 0.02	0.97 ± 0.01
FDis	7.54 ± 0.44 *	10.04 ± 0.91	8.96 ± 0.98 *	5.65 ± 0.67	14.01 ± 0.66 *	8.74 ± 1.00

Values are the mean ± standard error. Asterisks indicate a statistically significant difference between uninvaded and invaded plots in each forest type (* $p < 0.05$, ** $p < 0.01$). CF, coniferous forest; MF, coniferous and broadleaf mixed forest; EBF, evergreen broadleaf forest; S, richness; H, Shannon diversity; E, evenness; FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; FDis, functional dispersion.

3.2. Response of Soil Phosphorus Status to Invasion

The results of the two-way ANOVA demonstrated that the vegetation type and invasion had significant effects on soil TP, P fractions, and soil P sorption characteristics (Table 4). We found that the soil TP and soil P fractions (water-P, bicarb-Pi, and bicarb-Po) in the EBF and MF were significantly higher than those in the CF ($p < 0.05$). The soil P fraction between the invaded and uninvaded plots showed different response patterns to forest types. The soils in the invaded plots had higher bicarb-Pi and bicarb-Pothan those in the uninvaded plots in the MF and EBF, respectively (Figure 3). We did not find any significant differences in the biologically available P between the invaded and uninvaded plots in any of the forest types ($p > 0.05$).

The Langmuir model fit very well to the experimentally derived P sorption data, with a high coefficient of determination values. The average values of S_m and MBC predicted by the Langmuir equation were 1119 to 1792 mg/kg and 274 to 494 mg/kg, respectively. The soils in the uninvaded plots had higher S_m, MBC, and k than those in the invaded plots in the three forest types (Table 5).

Table 4. Results of the two-way analyses of variance for the effects of forest type (vegetation) and plant invasion (uninvaded vs. invaded) and their interaction on the soil phosphorus status.

	TP	Water-Pi	Bicarb-Pi	Bicarb-Po	S_m	MBC
Vegetation	38.59 ***	27.80 ***	245.85 ***	259.31 ***	6.65 **	14.14 **
Invasion	0.08	0.58	11.54 **	15.64 **	16.52 **	148.16 ***
Vegetation × invasion	0.41	1.61	8.71 **	0.77	1.23	0.24

** $p < 0.01$, *** $p < 0.001$. TP, total phosphorus; Water-Pi, water extracted inorganic phosphorus; Bicarb-Pi and Bicarb-Po represent the inorganic and organic phosphorus extracted by $NaHCO_3$; S_m, maximum of phosphorus sorption; MBC, maximum buffering capacity.

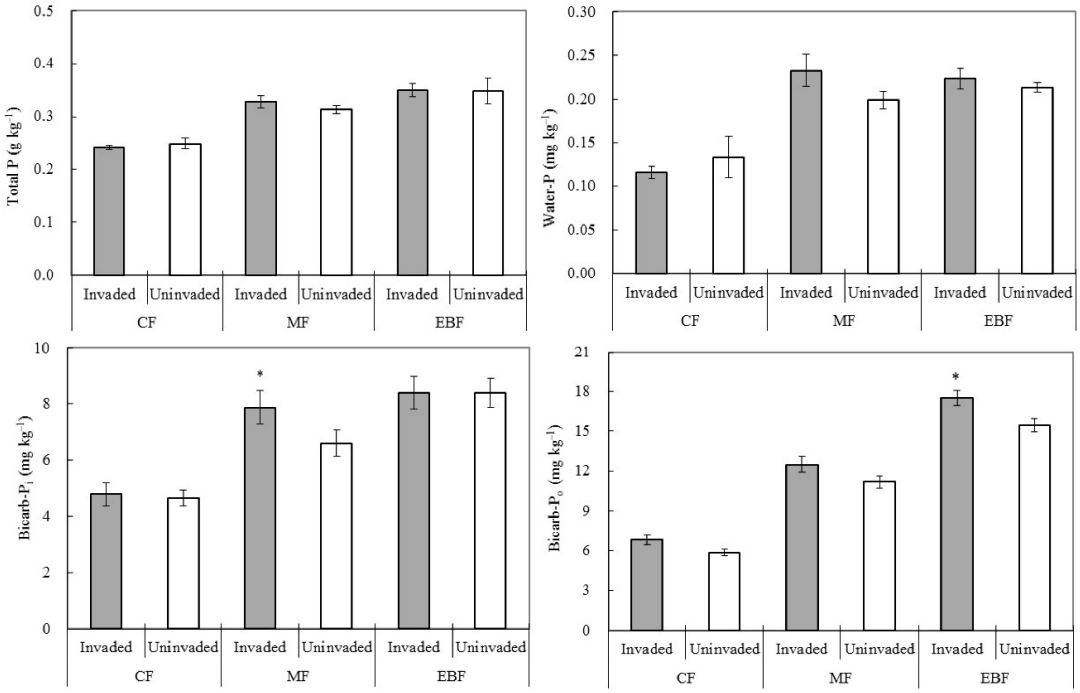

Figure 3. Comparison of the soil total P and P fractions in the invaded and uninvaded plots in the three forest types. Asterisks indicate a statistically significant difference between the uninvaded and invaded plots in each forest type (* $p < 0.05$). CF, coniferous forest; MF, coniferous and broadleaf mixed forest; EBF, evergreen broadleaf forest.

Table 5. Comparison of the P sorption characteristics between the invaded and uninvaded plots in the three forest types.

		k	S_m (mg kg^{-1})	MBC (mg kg^{-1})
CF	Invaded	0.25 ± 0.01	1119 ± 74 *	274 ± 22 **
	Uninvaded	0.27 ± 0.01	1570 ± 87	416 ± 11
MF	Invaded	0.21 ± 0.01 *	1467 ± 11	313 ± 16 **
	Uninvaded	0.29 ± 0.02	1632 ± 128	471 ± 10
EBF	Invaded	0.27 ± 0.02	1665 ± 126	448 ± 19
	Uninvaded	0.28 ± 0.01	1792 ± 74	494 ± 13

Values are the mean ± standard error. Asterisks indicate a statistically significant difference between uninvaded and invaded plots in each forest type (* $p < 0.05$, ** $p < 0.01$). CF, coniferous forest; MF, coniferous and broadleaf mixed forest; EBF, evergreen broadleaf forest; S_m, maximum of phosphorus sorption; MBC, maximum buffering capacity; *k*, binding energy.

3.3. Relationship between Understory Community Properties and Soil P Status

Our analyses revealed the strong effect of forest type on soil P status. Furthermore, invasion had a significant effect on bicarb-P and P sorption characteristics (Table 6). Overall, the relationship between

the understory community indices and soil P status was weak, yet some relevant patterns emerged: FRic was positively associated with TP, S was positively related to soil Sm, and H was negatively linked with bicarb-Pi, but only across invaded plots (Table 6). In addition, the invasion status affected four relationships: FRic-MBC and FDis-bicarb-Pi, which were closer in the invaded plots, and H-MBC and H-bicarb-Pi, which were stronger in the uninvaded plots (Table 6).

Table 6. Effects of understory community structure indices on the soil phosphorus status in the invaded and uninvaded plots (invasion) under the different forest types (vegetation).

Predictive Factors	TP	Water-Pi	Bicarb-Pi	Bicarb-Po	S_m	MBC
FRic	4.90 *	4.04	0.69	0.36	3.46	0.29
Vegetation	52.39 ***	25.50 ***	118.75 ***	201.60 ***	5.34 *	15.56 **
Invasion	4.38	0.88	7.48 *	1.71	1.40	26.76 ***
FRic × invasion						6.11 *
FEve	1.10	0.01	0.12	0.34	0.13	0.06
Vegetation	27.56 ***	11.22 **	62.62 ***	151.81 ***	4.99 *	11.49 **
Invasion	0.65	0.31	4.45	9.14 **	5.41 *	31.35 ***
FDiv	0.29	0.01	0.01	0.98	0.17	0.16
Vegetation	27.18 ***	18.27 ***	79.95 ***	187.41 ***	4.56 *	11.73 **
Invasion	0.19	0.41	4.53	17.07 **	7.32 *	36.33 ***
FDis	0.03	4.50	2.33	0.96	3.01	1.38
Vegetation	17.94 ***	20.10 ***	157.33 ***	130.37 ***	4.65 *	5.92 *
Invasion	0.29	0.16	15.72 **	0.28	0.22	14.52 **
FDis × invasion			12.20 **			
S	0.57	0.77	0.14	0.10	7.44 *	1.32
Vegetation	30.14 ***	20.25 ***	84.15 ***	189.40 ***	3.87 *	10.06 **
Invasion	0.44	1.19	4.31	9.35 **	2.42	24.56 ***
H	0.00	0.11	6.96 *	3.29	1.20	0.72
Vegetation	31.95 ***	32.12 ***	263.11 ***	221.16 ***	6.31 *	17.56 ***
Invasion	0.00	0.00	7.52 *	1.99	0.94	6.16 *
H × invasion			9.53 **			10.09 **
E	0.50	0.81	0.33	2.14	0.98	0.07
Vegetation	23.97 ***	18.87 ***	101.24 ***	158.59 ***	2.92	8.94 **
Invasion	0.27	0.09	3.60	1.68	0.27	2.36

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. TP, total P; Water-Pi, water extracted inorganic P; Bicarb-Pi and Bicarb-Po represent the inorganic and organic P extracted by $NaHCO_3$; S_m, maximum of P sorption; MBC, maximum buffering capacity; FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; FDis, functional dispersion; S, richness; H, Shannon diversity; E, evenness; GLM (general linear model) assessing the effect of predictive factors (interaction was only included when significant) on soil P status.

4. Discussion

4.1. Effects of Invasion on the Understory Community under Different Forest Types

The results demonstrate that there were large differences in the effects of forest type and invasion on the understory vegetation composition and functional characteristics, indicating that the extent of the response of understory vegetation to invasion depends on land cover type. Similar to other studies on the effect of invasion on community composition [12,22,37–39], we found that most of the analysed diversity indices, including S, FRic, FEve, and FDis, were altered by invasion. In subtropical regions of China, fast-growing species, such as coniferous species, are generally considered a pioneer stage of evergreen broadleaf climax forests that enhance the process of succession and improve the development of species diversity [40]. In the present study, the maximum decrease in FRic, FDiv, and FDis in the invaded plots (compared to the decrease in the uninvaded plots) was found in the CF; this pattern was related to both the local loss of native species and the introduction of an invasive species. In contrast, with the exception of FDis, in the MF and EBF, the functional diversity indices were not significantly

altered by invasion. These results indicate that the CF is more sensitive to invasion by *A. adenophora* than the MF and EBF. The low resistance to invasion in the CF was related to both the lower diversity of the understory community and site habitat. In particular, plots in the CF invaded by *A. adenophora* showed a notable reduction in species, as stated previously [22]. On the one hand, species-poor plant communities are more susceptible to invasion than species-rich communities, which is the argument of the classic diversity hypothesis [41]. On the other hand, the more widely available resource niches in the CF promote ecological invasion. For example, understory light conditions caused by the canopy characteristics of coniferous forests are conducive to invasion by light-demanding invasive species, such as *A. adenophora*. This explanation can be confirmed by the changes in functional diversity. This species loss was accompanied by obvious reductions in FRic and FDis. While FRic often depends on the number of species, FDis is independent of species richness [28,42]. The relatively low FDis in the invaded plots in the CF indicated that the species in the invaded plots are closer than those in the uninvaded plots to the centroid defined by all the species traits. However, the FDis increased in the invaded plots in the MF and EBF, indicating the abundances of species with trait values further away from the centroid of all species in the understory community trait space.

In addition to the FD indices, the nestedness analysis was used in our study to evaluate the species distribution patterns between the invaded and uninvaded plots. Some studies have reported that biotic homogenization is expected to lead to a nested pattern in species composition in the invasion process, i.e., species in highly invaded habitats are a subset of those present in less invaded habitats [43]. However, the nestedness analysis showed that the order of species loss under invasion was found only in the CF, suggesting that the understory community composition in the CF displays a gradual loss of species under invasion. According to community assembly rules, e.g., the biotic resistance hypothesis and environmental filtering hypothesis [44], abiotic stress or invasion may be the main filters for species, and native species that occupy trait spaces ecologically different from those of invasive species have a higher risk of loss (due to environmental filtering) in the CF plots (i.e., at an early successional stage). The maximum decrease in FRic, FDiv, and FDis was induced by invasion in the CF, which confirmed this assembly rule for the understory community. For the MF and EBF, competition may be the main filter for species establishment, and species with ecologically similar trait spaces to those of invasive species have a higher risk of loss [45,46]. In the mid- or late-successional stages, most species in understory communities tend to be more light-tolerant and share resource conservative strategies. However, *A. adenophora* is a light-demanding species with resource acquisition strategies [22]. *A. adenophora* invasion in the MF and EBF may have generated insignificant differences in the understory community composition and thus created a non-nested structure. This explanation was confirmed by the increase in the FDis in the invaded MF and EBF plots. Taken together, we can conclude that functional diversity is lower in the CF than in the other forest types due to the constrained functional traits induced by invasion and the limiting resource conditions. In the MF and EBF, niche partitioning because of competition for resources is functional and leads to higher FDis in the invaded plots.

4.2. Effect of Invasion on Soil P Status in Different Forest Types

Our study shows that invasion and forest type influenced P fractions and P sorption characteristics. Overall, in all the forest types, the invasion of *A. adenophora* increased the readily available P concentration (sum of water-Pi, bicarb-Pi and bicarb-Po), indicating that P mobilization in all the plots was likely enhanced. Several mechanisms may cause this increase. First, phosphorus is mobilized by root exudates, because organic acids secreted by roots can displace P from humic-metal complexes [47,48]. The decrease in soil pH in the invaded plots indirectly supported this explanation. Second, P mineralization may be enhanced by increased soil microbial activities. Some studies have reported that soil phosphatase activities increase in the sites invaded by *A. adenophora* compared to that in uninvaded sites [49]. Third, litter quality and the higher decomposition rate of invasive species supplied the amount of Po needed for mineralization by soil microbes. In addition, we found

significant differences in the TP and easily available P among the three forest types. This difference may be the result of litter quantity and quality and site conditions (e.g., the soil nutrients, soil microbial community, and microenvironment) [50]. According to the index of biologically available P in the soil proposed by Cross and Schlesinger [33], the values of this index were not significantly different between the invaded and uninvaded soils. However, the values of this index were significantly higher in the MF and EBF than in the CF, indicating that biological processes are more important for P cycling during succession. Invasion by *A. adenophora* did not significantly decrease or increase the role of biological processes in P cycling; however, the effect of this species will become prominent as the invasion intensity increases due to its competitive advantages in nutrient absorption and adaptive capacities. In the future, the abundance of *A. adenophora* will increase due to soil-plant feedback and will further affect the composition and functional attributes of understory communities.

Forest ecosystems have been identified as one of the major land cover types that can be used for controlling soil nutrient loss and preventing the eutrophication of water bodies. Our results showed that invasion and forest type significantly altered soil P sorption characteristics. In general, the P loss was small from soils with higher S_m and MBC values. In this study, we found that the soils in the uninvaded plots and later successional stages had greater S_m and MBC values than those in the invaded plots and early- or mid-successional stages. Generally, the value of S_m varies as a function of Al/Fe, SOC, pH, and soil clay content [51–53]. In this study, although the SOC was significantly correlated with the S_m, soil exchangeable Al and Fe are considered direct indicators of P retention in soils [52]. Previous studies have reported that significantly lower Fe and Al were recorded within the soils in invaded sites and early-succession stages than in soils from uninvaded sites and late-succession stages [15,54]. Although invasion increases the risk of soil P loss potential, higher S_m and MBC values indicate that forests are one of the suitable land cover types for controlling soil P loss among the different landscape types in this region.

4.3. Relationships between Understory Vegetation and Soil P Status

In forest ecosystems, understory vegetation plays a critical role in ecosystem processes and functioning. For example, several studies have reported that the understory has a greater effect than the tree layer on soil microbes [13,14]. Similarly, P cycling is influenced by different understory communities, which cause strong changes in soil physicochemical and biological properties [52,55,56]. In our study, we found that soil P status was more sensitive to forest type and invasion than to the functional properties of the understory community. First, the effect of different vegetation types on soil P content has been previously reported in many studies. For example, Fu et al. reported that soil P fraction distributions and their dynamics were significantly influenced by different vegetation restoration types [50]. The difference in the distribution of soil P fractions can be attributed to changes in the species composition and functional attributes of the plant community, as well as the soil microbial community [18,52]. Second, we found a strong impact of invasion on the soil P status, especially the bicarb-Pi, bicarb-Po and P-sorption indices, but an inconsistent impact on different soil P indices. Turrión et al. reported that labile Pi forms were influenced to a greater extent than organic P forms by vegetation cover [56]. However, our results partly contradicted those of previous studies. In addition to soil bicarb-Pi, bicarb-Po was also sensitive to vegetation cover and invasion. The effect on soil bicarb-Po may be attributed to the difference in the SOC and litter quantity and quality between the invaded and uninvaded plots in the different forest types.

In the present study, weak relationships were found between the species and functional indices of the understory communities and the soil P status, suggesting that the response rates to invasion, i.e., the time lag between the changes in the understory community and soil P properties, were different in each forest ecosystem. For example, it may take several years or decades to change the functional attributes or species composition of the understory in an invaded forest due to different plant life forms or life-history traits. Similarly, the response time of soil labile P fractions to the external environment varies from a few hours (water-Pi and bicarb-Pi) to several years (bicarb-Po). In addition, other factors,

such as the accumulation of SOC before the invasion and duration of invasion by *A. adenophora*, may contribute to explaining the weak relationship between the understory community and soil P status [57].

Although we lack information on invasion times and the habitat conditions before invasion, our results still showed that several plant community indices (FDis and H) can be used to predict and assess the changes in soil P status. In the invaded plots, the FDis was positively associated with soil bicarb-Pi, indicating an increase in viable plant life strategies following invasion. According to the complementary niche hypothesis, our results suggest that the niche space increases with invasion, which supports the higher trait dispersion to exploit limited P resources more efficiently. Conversely, the Shannon diversity index of the understory communities was negatively linked with soil bicarb-Pi in uninvaded plots, suggesting a higher depletion of soil-available P by more species in the early- and mid-successional stages. In addition, we found that the FRic and H were closely associated with the soil MBC. Because MBC is affected by many factors, such as pH, clay content, SOC, organic acid, and Fe and Al content [51–53], more data are needed to further understand the complex relationships among invasion, community properties, and soil P sorption characteristics.

5. Conclusions

The results demonstrate that the species diversity and functional diversity of the understory community significantly varied by vegetation type. Among the invaded plots, the largest decreases in the FRic, FDiv, and FDis and biotic homogenization were found in the CF rather than in the MF or EBF. Furthermore, the invasion of *A. adenophora* significantly increased the soil bicarb-Pi and Po in the MF and EBF, respectively, while it obviously decreased the soil S_m and MBC in the CF. In addition, we found that the soil P status was more sensitive to the forest type and invasion than to the functional properties of the understory community. These changes in species and the functional attributes of the understory communities were weakly associated with changes in the soil P status, probably due to the different response times to invasion in different forest types.

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